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·热点评述·

植物细胞质外体pH感受机制的解析

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摘要 质外体是植物感受和应答环境胁迫(包括生物和非生物胁迫)的前沿区域。质外体的pH值是被严格调控的重要生理参数。环境胁迫(如细菌病害)等会引起植物细胞质外体碱化现象。然而，质外体pH如何协调根生长与免疫响应？其分子调控机制尚不清楚。最近，南方科技大学生命科学学院郭红卫团队与清华大学-德国马克斯普朗克研究所-科隆大学柴继杰团队以模式植物拟南芥(*Arabidopsis thaliana*)为研究材料，通过遗传学、细胞生物学、生物化学和结构生物学等综合手段，发现细胞表面小肽-受体复合物可作为质外体pH感受器，感受和应答分子模式触发的免疫(PTI)引发的拟南芥根尖分生组织细胞质外体碱化。该研究揭示了植物根尖分生组织细胞质外体pH感受的蛋白质复合物及响应机制，以及免疫与生长之间的协调机制，加深了人们对植物如何平衡生长与免疫应答生物学反应过程的理解。

关键词 拟南芥，质外体pH，感受器

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植物不像动物那样遇到不利的环境条件可以躲避。因此在长期的适应过程中，植物进化出使其在不断变化的环境中快速反应的生存机制。外部环境信号被转化为细胞间和细胞内信号，通过协调生长、发育以及胁迫应激反应来适应环境胁迫。由细胞原生质体外围细胞壁、细胞间隙和导管组成的质外体系统，存在于植物的根、茎和叶等器官中，是水和溶质在植物体内运输的通道。质外体同时也是物质运输、植物与微生物相互作用、信号转导以及对环境胁迫做出适应性反应的重要空间。因此，质外体成为植物感受和应答环境胁迫(包括生物和非生物胁迫)的前沿区域。

质外体pH值对于植物细胞的生命活动至关重要。正常条件下，植物质外体保持弱酸性状态，pH值范围通常在5.5–5.7之间(Blumwald et al., 2000; Barbez et al., 2017; Martinière et al., 2018)，而细胞质保持弱碱性，pH值通常在7.0–7.4之间(Blumwald et al., 2000; Martinière et al., 2018)，这样内(细胞质)碱外(质外体)酸，就形成了跨质膜的质子梯度和电化学梯度，为物质的跨膜运输提供驱动力。质外体的pH值由质膜H^+-ATPase引起的H^+外流和H^+依赖转运体引起的H^+内流决定(Yang and Guo, 2018; Havshøi and Fuglsang, 2022; Li et al., 2022)。蛋白激酶TMK1 (TRANSMEMBRANE KINASE 1)响应生长素信号，磷酸化并激活质膜H^+-ATPase活性，导致质外体酸化，促进细胞生长(Cao et al., 2019; Li et al., 2021; Lin et al., 2021)。而在病原微生物入侵等逆境条件下，质外体会发生碱化，该现象在病原菌入侵的几分钟内发生，并持续几十小时(Bacon et al.,1998; Huffaker and Ryan, 2007; Geilfus et al., 2017)，这种持久的碱化被认为可最大限度地减少病原微生物的生长并增强宿主抗性(Felle et al., 2004, 2005)。质外体碱化作为一种重要信号在植物体内转导胁迫信息，不同激发子激活植物免疫后通常伴随生长抑制，这对于植物应答胁迫至关重要。尽管人们在20世纪90年代就发现了植物激发免疫反应会引起细胞质外体碱化现象，然而免疫胁迫引起质外体碱化的生物学意义仍是未解之谜，其分子调控机制也不清楚。尤其是病原菌入侵导致的植物细胞质外体碱化现象如何被感知？信号如何传递到胞内？这些都是亟待解决的科学问题。

近20年的研究发现，一些分泌小肽在细胞生命

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活动过程中行驶关键的生理功能。类似于传统的植物激素，这些小肽被认为是植物激素样信号分子——植物细胞因子，植物细胞因子的概念现在被广泛接受(Motomitsu et al., 2015)。大多数植物细胞因子含有信号肽序列，这些信号肽序列在基于胞吐作用的分泌和细胞外运输过程中被切割。一些植物细胞因子经过进一步的翻译后修饰(如糖基化、酪氨酸硫酸化或形成二硫键)以形成正确的三维结构，进而形成有活性的小肽。小肽在传递信号时，最初大多由受体蛋白接收并依次传递到靶标分子(Osakabe et al., 2013)。动物中最主要的细胞表面受体为酪氨酸受体激酶(receptor tyrosine kinase, RTKs)。植物体内最重要的受体是类受体激酶(receptor-like kinase, RLKs)，它们在细胞间以及在植物与环境的通讯中发挥重要作用。

最近，郭红卫团队和柴继杰团队在模式植物拟南芥(*Arabidopsis thaliana*)中发现，细胞表面小肽-受体复合物可以作为质外体pH感受器，感受和应答分子模式触发的免疫(pattern triggered immunity, PTI)引发的拟南芥根尖分生组织细胞质外体碱化(图1) (Liu et al., 2022)。研究表明，用植物激发子小肽Pep1 (plant elicitor peptide 1)处理植物时，根尖分生区细胞质外体pH值迅速升高，并且Pep1激发的免疫反应抑制了根尖分生组织生长，通过抑制促进根干细胞生长的小肽激素RGF1 (root meristem growth factor 1)信号通路，降低根尖生长发育关键转录因子PLT1/2的表达。研究人员模拟免疫反应引起的胞外碱化，证实胞外碱化抑制RGF1信号通路，表明RGF1信号通路能够响应胞外pH变化。综上所述，该研究发现，在正常条件下，RGF1感受植物细胞质外体酸化状态，与RGFRs (cell-surface peptide-receptors)结合，促进根尖分生组织的生长；在PTI引发的根尖分生组织细胞质外体碱化发生时，一方面，RGF1与RGFRs的结合受到抑制，另一方面，PEPRs (RGF receptors)感受质外体pH的碱化，pH的碱化促进Pep1与PEPRs结合，引发免疫应答反应。上述两类感受器分别感受质外体的pH，进而调控相应的信号通路，协调植物的免疫与生长发育。

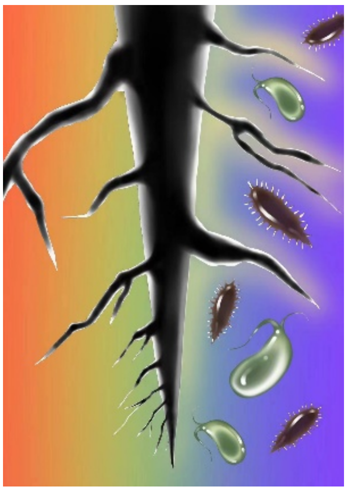

图1　分子模式触发的免疫(PTI)引发的拟南芥根尖分生组织细胞质外体碱化现象感受示意图(郭红卫教授提供)

Figure 1　Schematic diagram of the perception of apoplast alkalinization in *Arabidopsis* root apical meristem induced by pattern triggered immunity (PTI) (provided by Prof. Hongwei Guo)

该研究首次发现了植物细胞质外体pH的感受器，揭示了长期以来人们所关注的病原菌等逆境引起的质外体碱化的一种生物学意义，阐明了质外体碱化的感受机制以及植物协调免疫与生长发育的机制，使人们深刻理解植物如何精准调控自身代谢以及平衡生长与免疫应答的生物学过程。该研究揭示的植物细胞“酸碱调控”机制也为通过分子设计育种提高作物产量和耐逆性奠定了理论基础。

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Analysis of the pH Sensing Mechanism of Plant Apoplasts

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Abstract The apoplast is the frontier area for plants to sense and respond to environmental stresses (including biotic and abiotic stresses). The pH of the apoplast is an important physiological parameter that is tightly regulated. Environmental stress (such as bacterial disease) can cause alkalinization of plant apoplast, but how does apoplast pH coordinate root growth and immune response? Its molecular regulation mechanism is still unclear. Recently, the team of Professor Hongwei Guo from the School of Life Sciences, Southern University of Science and Technology, and the team of Professor Jijie Chai from Tsinghua University-Max Planck Institute of Germany-University of Cologne used the model plant *Arabidopsis* as research materials, through genetic, cellular, biochemical and structural biology. By means of comprehensive methods, it was found that the small peptide-receptor complex on the cell surface can act as an apoplast pH sensor to sense and respond to the apoplast alkalinization of *Arabidopsis* root apex meristem cells induced by pattern triggered immunity (PTI). The results of this research have discovered the protein complex and response mechanism of plant root apex meristem apoplast pH sensing, as well as the coordination mechanism between immunity and growth, further understanding the biology reaction process of how plants balance growth and immune response.

Key words *Arabidopsis thaliana*, apoplast pH, receptor

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